

LOWER CRETACEOUS AMMONITES FROM
NORTH-EAST ENGLAND: THE HAUTERIVIAN
HETEROMORPH *AEGOCRIO CERAS*

BY

PETER FRANKLIN RAWSON

Department of Geology, Queen Mary College, University of London

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ABSTRACT

Aegocrioceras is a common heteromorph ammonite in the Speeton Clay of Filey Bay, Yorkshire, where seven species occur, of which *A. compressum* and *A. spathi* are described herein as new. Another two species are provisionally included in the genus. A neotype of *A. ravicostatum* (Phillips 1829) and a lectotype of *A. torulosum* (Koenen 1902) are designated. The stratigraphical horizons of most species have now been established: six are limited to parts of Bed C7, in which three discrete assemblage occur in a thickness of only 2.6 m of clay. The faunal and sedimentary sequence is condensed and probably incomplete. *A. ? seeleyi* occurs higher in the succession, in Bed C4L, and *A. ? koeneni* is probably from the same horizon.

The type species of *Aegocrioceras*, *A. capricornu* (Roemer), is not known from Speeton, but some north German examples are discussed. There are great similarities between the faunas of the two areas although the stratigraphy of the German faunas is still poorly known.

I. INTRODUCTION

Aegocrioceras is a distinctive capricorn heteromorph ammonite of mid-Hauterivian age, which is apparently endemic to north-west Europe. Although it is represented by abundant and varied forms, the sequence of species has never been established and the taxonomy is confused; the confusion is emphasized by Spath's (1924) list (see p. 155) of the Speeton fauna in which over 20 taxa are recorded, many under unpublished names or as the misidentifications of earlier authors.

The sequence of species in the Speeton Clay, and the variation they exhibit, has been assessed as a result of the bed-by-bed collection of over 150 specimens. This collection has been divided between the British Museum (Natural History) and the University of Hull. Existing museum and private collections have also been studied and the more important specimens are referred to here. The research forms part of a study commenced during the tenure of a N.E.R.C. research studentship at the University of Hull and continued at Queen Mary College, partly during the tenure of a N.E.R.C. post-doctoral fellowship. Study of comparable faunas in Germany was assisted by awards from the Daniel Pidgeon Fund of the Geological Society of London (1969), the Central Research Fund of the University of London (1971) and the European Exchange Programme between the Royal Society and the Deutsche Forschungs-Gemeinschaft (1973).

I thank Dr E. Kemper and Dr Fr. Schmid (Hanover), Dr C. Spaeth (Hamburg), and the numerous colleagues mentioned in the first paper of this series (Rawson 1971a) for their considerable assistance, and Dr F. A. Middlemiss (Queen Mary College) for reading the manuscript.

II. PREVIOUS WORK ON THE SPEETON AEGOCRIOCERAS

Even as early as 1868, so much confusion was caused by the use of ill-defined names that Judd (1868: 247-248), discussing the Speeton '*Ancyloceras*' (*Aegocrioceras*, *Crioceratites* and allies), warned 'in the large majority of instances, we find at Speeton small and detached fragments of a single whorl only, which for the purposes of identification and description are absolutely worthless, and which, if so made use of, can only be sources of error. For these reasons I think that the various species of this group, founded by Young and Bird, Phillips and Römer, generally on the smallest fragments, might with no loss, but much positive advantage, to palaeontology be suppressed.'

Of the authors that Judd referred to, Young & Bird (1828) only described one species of *Aegocrioceras*, *A. bicarinatum*, which has now been stabilized by the selection of a neotype (Howarth 1962). The specific names used by John Phillips are less problematic than subsequent usage (e.g. Koenen 1902; Spath 1924) has implied, for Phillips (1829) clearly referred most of his figured specimens to species already described by the Sowerbys. Though he eventually (Phillips 1875) expressed doubt on the identification of the Speeton forms with the Sowerby species, the specific names cannot be attributed to Phillips. Only one genuinely new name, *Hamites varicostatus*, can be referred to *Aegocrioceras*: a neotype for this species is now designated (see p. 143). Roemer (1841) described several new '*Hamites*', of

which three, *Hamites subnodosus*, *H. semicinctus* and *H. capricornu*, belong to *Aegocrioceras*. The types are lost, but *A. semicinctum*, based partly on a Speeton specimen, is readily identifiable from Roemer's description and figure. *A. capricornu*, though frequently recorded and utilized as a zonal index in north Germany, is much more difficult to interpret and German stratigraphers have used it as a 'sack' name for any of the more compressed *Aegocrioceras*.

Buckland (1836) published a manuscript name of Phillips, *A. bucklandi*, which was used by most early collectors. A very active amateur at that time was William Bean (1787–1866), who originated several manuscript names (Rawson 1970 : 590) which enjoyed a wide circulation among contemporary collectors. The names are still visible on labels (sometimes in Bean's handwriting) in his own and other (e.g. Bowerbank's, Lady Hastings') collections : all were recorded in Spath's (1924) faunal list. One Bean manuscript name, *A. quadratum*, was eventually published by Crick (1898) and the lectotype of this species has now been described and refigured (Rawson 1970 : 585).

Despite the number of published and Bean manuscript names already familiar to the early and mid-nineteenth-century collectors, very few were listed in the essentially stratigraphical works of Leckenby (1859), Judd (1868) and Lamplugh (1889). All three authors referred to the occurrence of various '*Hamites*' or '*Crioceras*' and recognized two distinct horizons (Beds C7F and C7A of the modern nomenclature) characterized by large heteromorphs now assigned to *Aegocrioceras* and *Crioceratites*. Both Judd (1868) and Lamplugh (1889) stressed the difficulty of identifying the heteromorphs, and Judd's opinion has already been quoted.

Pavlov (1892) figured one of Lamplugh's specimens and noted that the fragments of '*Crioceras*' which he had examined suggested rather a diverse fauna. However, Danford's (1906) subsequent review of the Speeton ammonites shed little new light on this, for it included only a brief note on the heteromorphs. The three listed species referable to *Aegocrioceras* were identified by Dr A. von Koenen, who had earlier (Koenen 1902) made brief note of some Speeton forms. Spath's (1924) list of Speeton *Aegocrioceras* is essentially a compilation of records from existing collections and does not represent a critical revision of the fauna. The interpretation of some of the listed forms has recently been discussed (Rawson 1970) and is further elaborated upon in the appendix (p. 154).

Despite these numerous references to the Speeton *Aegocrioceras*, Pavlov's (1892) suggestion that the fauna would merit a more detailed palaeontological study has gone unheeded. A similar situation prevails in north Germany, where Roemer's (1841), Neumayr & Uhlig's (1881) and especially Koenen's (1902) monographs drew attention to the rich faunas of the 'capricornu-Schichten', yet stratigraphers have continued to 'lump' the various forms into three broad 'species', *A. semicinctum* (Roemer), *A. torulosum* (Koenen) [= *A. quadratum* (Crick)] and *A. capricornu* (Roemer).

III. LITHOSTRATIGRAPHY

Lamplugh's (1889) main subdivisions of the Speeton Clay and Fletcher's (1969) lithostratigraphical subdivision of the C Beds have been discussed in detail in an

earlier paper (Rawson 1971a). With the exception of two species only questionably included in *Aegocrioceras*, the genus is apparently limited to Beds C7G to C7A, occurring through a vertical thickness of only 2.6 m of clay. No *Aegocrioceras* are known from the overlying Beds C6 and C5, but *A. ? seeleyi* (Neumayr & Uhlig) appears in Bed C4L and *A. ? koeneni* Spath is probably from this horizon.

The lithological subdivision of Bed C7 is as follows :

Bed		Thickness (metres)
C7A	Brown-weathering, silty, indurated clays with large calcareous lenticles, often partially phosphatized. <i>Crioceratites</i> spp., <i>Aegocrioceras spathi</i> sp. nov.	0.30
C7B	Pale grey clay. <i>A. spathi</i> sp. nov.	0.30
C7C	Dark grey clay with large pale mottles (<i>Chondrites</i>) at top	0.38
C7D	Pale grey clay with a little glauconite. <i>A. varicostatum</i> (Phillips), <i>A. compressum</i> sp. nov.	0.30
C7E	Black clay; large, pale grey mottles (<i>Chondrites</i>) at top. Glauconite abundant at top, diminishing downwards. <i>A. compressum</i> sp. nov.	0.38
C7F	Pale grey clay with abundant flattened <i>Simbirskites</i> (<i>Speetonicerases</i>) sp.	0.15
	Pale grey, silty clay, weathering brown and locally indurated. Contains round, phosphatized nodules (up to 150 mm diameter) often enclosed in larger, more irregular calcareous concretions. Body chambers of <i>Aegocrioceras</i> are common, especially in the calcareous concretions. <i>A. quadratum</i> (Crick), <i>A. semicinctum</i> (Roemer), <i>A. bicarinatum</i> (Young & Bird), <i>Simbirskites</i> (<i>Speetonicerases</i>) sp.	0.23
C7G	Pale grey clay with <i>Chondrites</i> . <i>A. quadratum</i> (Crick), <i>A. semicinctum</i> (Roemer), <i>A. bicarinatum</i> (Young & Bird), <i>S. (Sp.) inversum</i> (M. Pavlow)	0.53
C7H	Dark grey clay with abundant glauconite. <i>S. (Sp.) inversum</i> (M. Pavlow), <i>S. (Sp.)</i> cf. <i>versicolor</i> (Trautschold)	0.30

These subdivisions are summarized in Text-fig. 2 (p. 151).

IV. SYSTEMATIC DESCRIPTIONS

Morphological terms used in the systematic descriptions are defined in the ammonoid volume of the *Treatise on Invertebrate Paleontology* (Arkell *et al.* 1957: L2-L6).

Because of the fragmentary nature of most specimens, few parameters can be measured for statistical purposes. However, the ratio of whorl thickness to whorl height (wt/wh) can be obtained even for small fragments and expresses the relative compression of the whorl section (Table 1). For specimens above an estimated diameter of 10 mm the ratio shows no significant change during growth.

TABLE 1

Ratio of whorl thickness (wt) to whorl height (wh), for seven species of *Aegocrioceras*

Species	Number of specimens measured	Mean wt/wh
<i>semicinctum</i>	14	0.96
<i>quadratum</i>	46	0.92
<i>bicarinatum</i>	42	0.91
<i>spathi</i>	7	0.78
<i>varicostatum</i>	15	0.74
<i>densiradiatum</i>	3	0.71
<i>compressum</i>	7	0.67

The nature of the information included in certain sections of each specific description is outlined here.

Synonymy

With few exceptions, only papers in which specimens are illustrated are referred to in the synonymy. Reference is not normally made to Spath's (1924) faunal list, for although this has hitherto been the standard reference for the Speeton sequence there are considerable problems in interpreting the identifications in the absence of figures or descriptions; a partial reinterpretation of Spath's records is included as an appendix to this paper (p. 154).

Certain symbols have been used to provide a more critical synonymy, as follows:

- v (vidimus) specimen seen by the author
- v* type specimen seen
- d (deletum) specimen is lost
- d* type specimen is lost

Material

The majority of the described specimens were collected by the author and are now in the British Museum (Natural History) (BM.) and the University of Hull (HU.Rn.). Additional specimens in other collections have been utilized where necessary, though the exact horizons of most are not recorded. These are from the following collections: British Museum (Natural History) (BM.), Hull Museum (HM.), the Museum of the Institute of Geological Sciences (GSM.); the Geologisches-Paläontologisches Institut, Göttingen (GPiG.); the Niedersächsisches Landesamt für Bodenforschung, Hanover (NLfB.); the Sedgwick Museum, Cambridge (SM.); the Yorkshire Museum, York (YM.); the University of Hull (HU.); and the private collection of Messrs C. W. and E. V. Wright (Wrights' collection).

The descriptions are based on 221 Speeton specimens, together with 12 north German specimens used for comparison. The 233 specimens are distributed among 10 species, as shown in Table 2.

TABLE 2

Distribution of the specimens studied among ten species of *Aegocrioceras*

Species	Number of specimens (including type)	
	Speeton	North Germany
<i>A. bicarinatum</i> (Young & Bird)	39	—
<i>A. quadratum</i> (Crick)	70	1
<i>A. semicinctum</i> (Roemer)	22	—
<i>A. varicostatum</i> (Phillips)	45	3
<i>A. compressum</i> sp. nov.	4	2
<i>A. spathi</i> sp. nov.	17	3
<i>A. densiradiatum</i> Rawson	8	—
<i>A. capricornu</i> (Roemer)	—	3
<i>A. ? seeleyi</i> (Neumayr & Uhlig)	5	—
<i>A. ? koeneni</i> Spath	11	—
	—	—
	221	12

Dimensions of figured specimens

Where possible, the dimensions of figured specimens are given. Because the specimens are uncoiled, the distance between the dorsum of the last whorl and the venter of the preceding whorl is included in addition to the standard measurements. Dimensions (in millimetres) are therefore listed as follows – diameter : whorl height, whorl thickness, width of umbilicus, distance between dorsum and venter. These are followed by the number of ribs on the last whorl ; (e) = estimated dimension or rib number.

Suborder **ANCYLOCERATINA** Wiedmann 1966

Superfamily **ANCYLOCERATACEAE** Meek 1876

Family **ANCYLOCERATIDAE** Meek 1876

Subfamily **CRIOCERATITINAE** Wright 1952

The Crioceratitinae include a series of crioceratitid and small ancyloceratid heteromorphs of late Valanginian to Barremian age, together with normally coiled derivatives such as *Pseudothurmannia* and *Hemihoplites*. The heteromorph and normally coiled genera are linked by morphological transitions (Wiedmann 1962, 1969) and possess similar sutures with quadrilobate primary suture and characteristic I-U-L-E lobe formula throughout growth (Wiedmann 1969).

There are two main schools of thought concerning the origin of the Crioceratitinae. The sculptural resemblance and stratigraphical relationship between early Crioceratitinae and some of the immediately preceding, evolute *Acanthodiscus* and partly uncoiled *Distoloceras* led many of the earlier workers (e.g. Neumayr & Uhlig 1881 ; Kilian 1910) to derive the majority of the Crioceratitinae from the Neocomitinae ; this view was upheld by Sarkar (1955). On the other hand, sutural characteristics and the uncoiled shell of the Crioceratitinae suggest a close relationship with earlier heteromorphs and with the lytoceratid ammonites (Wright 1957 ; Thomel 1964). Wright (1957), Thieuloy (1965) and Wiedmann (1969) derived the Crioceratitinae monophyletically from the Protancyloceratinae. Wiedmann (1969) has put forward strong arguments for a monophyletic origin of all the 'Cretaceous' heteromorphs, placing them in the Suborder Ancyloceratina Wiedmann 1966. The earliest (Middle Tithonian) representatives are probably derived from a lytoceratid, though intermediate forms are not known (Wiedmann 1973 : 313).

The earliest Crioceratitinae appear to be the north German genus *Juddiceras* Spath and the southern French *Himantoceras* Thieuloy, both of Upper Valanginian age. I regard *Juddiceras* as a primitive crioceratitid rather than a late protancyloceratid because of its similarity to *Himantoceras acuticostatum* Thieuloy. *Himantoceras* was originally dated as basal Hauterivian (Thieuloy 1965) but has subsequently been assigned to the Upper Valanginian (Moullade & Thieuloy 1967 ; Thieuloy 1973).

Genus **AEGOCRIO CERAS** Spath 1924

TYPE SPECIES. *Hamites capricornu* Roemer 1841, by original designation.

DIAGNOSIS. A genus with crioceratitid coiling and strong, single, radial ribs. Tubercles, mainly ventro-lateral, are common in juveniles but disappear with growth.

DESCRIPTION. The maximum diameter is at least 500 mm, the body chamber occupying $\frac{1}{2}$ to $\frac{2}{3}$ of a whorl. Coiling is crioceratitid throughout; adjacent whorls may be almost in contact or well separated. The whorl section is rounded to subquadrate, inflated to compressed, the dorsum varying from slightly impressed to slightly convex. Ornament consists of strong, single, rectiradiate, prorsiradiate or rursiradiate, straight or curved ribs which extend across the venter without interruption but are usually represented on the dorsum by forwardly curving, feeble rib-folds. The dorsum is also crossed by well-defined growth striae, which are less clearly visible on flanks and venter. On the early whorls small ventro-lateral tubercles are generally present on most ribs; these disappear with growth. In one species (*A. semicinctum*), mid-lateral and sometimes dorso-lateral as well as ventro-lateral tubercles occur on occasional ribs in early growth stages.



FIG. 1. Suture lines of *Aegocrioceras*. a, *A. bicarinatum* (BM. C78926).
b, *A. quadratum* (BM. C79042). c, *A. varicostatum* (HU.Rn. 874).

The primary and first few subsequent sutures are not known, but the juvenile to adult growth stages have a quadrilobate suture. Each saddle is usually fairly deeply subdivided by a single, long lobelet, and adjacent sutures are normally in contact at their extremities, except in *A. varicostatum*.

DISCUSSION. Spath (1924:76) introduced the generic name for a distinctive group of north-west European capricorn crioceratitids 'differing from *Crioceras* s.s. (*duvali* group) in ornament and suture-line'. The latter part of his statement cannot be supported, but the strong, relatively uniform simple ribs clearly differentiate *Aegocrioceras* from *Crioceratites* with its periodic stronger, bi- or tri-tuberculate ribs.

The origin of *Aegocrioceras* is problematic. In north-west Europe, no *Criocera*-tinae are known from the Lower Hauterivian *Endemoceras* beds, but *Aegocrioceras* appears suddenly, and in abundance, just above. Although this suggests an immigration from elsewhere there are no obvious immediate ancestors in France, where the Lower Hauterivian *loryi* group are typical *Crioceratites* (Thieuloy 1972 : pl. 5), or in any other known Lower Hauterivian faunas. It is possible that, despite the time gap, *Aegocrioceras* is a derivative of the Upper Valanginian *Juddiceras*, which occurs in north Germany.

The Tethyan genera *Leptoceras* Uhlig, of Berriasian and Valanginian age, and the homeomorphic *Leptoceratoides* Thieuloy from the Barremian are similar in general morphology to *Aegocrioceras*, but both are microconch genera growing to only about 30 mm diameter. The early identification of some Speeton *Aegocrioceras* with the French '*Crioceras*' *puzosianum* d'Orb. (e.g. Judd 1868) indicates at least a superficial similarity with another Tethyan form, though the latter is so poorly known that the true relationship remains obscure. Sarkar (1955 : 160) questionably included d'Orbigny's species in his new genus *Spathicrioceras*, but was unable to locate the type or any other example. He considered the age to be Barremian, 'after Kilian'. Uhlig (1883) thought the species was like a '*Leptoceras*', but d'Orbigny's figure could equally well be interpreted as an *Aegocrioceras* : in the absence of further material it is impossible to decide whether '*C.*' *puzosianum* is a *Spathicrioceras*, *Leptoceras*, *Leptoceratoides* or *Aegocrioceras*.

As 'genotype' of *Aegocrioceras*, Spath (1924 : 76) proposed "'*Crioceras*" *capricornu* (Roemer) Pavlow (1892)'. This creates an immediate problem as Pavlow's (1892 : 154, pl. 18, fig. 9) '*capricornu*' belongs to *A. bicarinatum* (Young & Bird). It seems from the complicated taxonomic procedure followed throughout his paper that Spath regarded Roemer's (1841) and Pavlow's (1892) '*capricornu*' as the same species, and this is also apparent from some of the extant specimens bearing Spath's identifications. He apparently referred to Pavlow's figure rather than Roemer's because Pavlow's was much the better. Therefore according to I.C.Z.N. rules, *A. capricornu* Roemer, not *A. bicarinatum* (Young & Bird) (= '*capricornu*' Pavlow 1892), must be taken as the type species.

Aegocrioceras bicarinatum (Young & Bird)

Fig. 1a ; Pl. I, fig. 2 ; Pl. 2, fig. 1

- d* 1828 *Hamites bicarinatus* Young & Bird : 278, pl. 15, fig. 10.
- v ? 1829 *Hamites alternatus* Sowerby ; Phillips : 123, pl. 1, fig. 27 (non fig. 26). (2nd edit. 1835 ; 3rd edit. 1875).
- d 1892 *Crioceras capricornu* (Roemer) ; Pavlow : 154, pl. 19, fig. 9.
- d 1902 *Crioceras capricornu* (Pavlow non Roemer) ; Koenen : 320.
- v 1906 *Crioceras matheroni* d'Orbigny ; Koenen in Danford : 113.
- v 1924 *Aegocrioceras subseeleyi* Spath : 77.
- v 1962 *Aegocrioceras bicarinatum* (Young & Bird) Howarth : 209, pl. 19, fig. 8.
- v 1969 *Aegocrioceras bicarinatum* (Young & Bird) ; Hiltermann & Kemper : 23, pl. 2, figs 1, 2.
- v 1970 *Aegocrioceras subseeleyi* Spath ; Rawson : 587, figs 3-5.

TYPE. BM. 89107 (Bean collection), from the Speeton Clay of Speeton, was designated neotype and figured by Howarth (1962).

MATERIAL. 38 specimens (author's collection) from Speeton, mainly whorl fragments: 35 from Bed C7G (BM. C78926-78949; HU.Rn. 702-704, 933, 1031, 1065, 1100, 1106, 1166, 1200, 1211) and 3 from Bed C7F (HU.Rn. 367, 585, 935). There are about 20 specimens in the museum collections.

DESCRIPTION. The whorl is higher than wide ($wt/wh = 0.91$), with a subquadrate whorl section. The flanks are gently rounded, angular at the ventro-lateral edge and rounded in the dorso-lateral region; the dorsum is flat or gently rounded. The whorl height increases fairly slowly. The ribs are single, sharp, rectiradiate or prorsiradiate and extend straight across the venter. Above about 35 mm diameter the ribs bend forward more strongly about two-thirds of the way over the whorl flank (Pl. 1, fig. 2). In the earlier growth-stages they bear feeble tubercles on the ventro-lateral edge; at first these are developed on every second or third rib, but above about 10 mm diameter they occur on every rib. They diminish and eventually disappear above about 35-40 mm diameter. The number of ribs per whorl increases gradually with growth; at diameters of 30-40 mm the estimated number varies between 35 and 45, while in the specimen of 48 mm diameter figured on Pl. 1, fig. 2, there are 43 ribs on the last whorl.

DIMENSIONS of figured specimens:

BM. C78933 (Pl. 1, fig. 2) 52.1. At 48.0: 15.8, 14.2, 23.5, 3.4. 43 ribs.

GSM. 17540 (Pl. 2, fig. 1) 27.4: 9.6, 7.5, 13.0, -. 35 ribs.

DISCUSSION. Young & Bird's (1828) original description is adequate though their figure is poor; the specific name was not used by subsequent authors (or by the early collectors) with the exception of Spath (1924: 78), who thought that it referred to a *Paracrioceras* from the B Beds. Howarth (1962: 209) reinterpreted *Hamites bicarinatus* as a species of *Aegocrioceras* and proposed a neotype. Spath's (1924: 77) record of '*A. intermedium* (Bean MS non Phillips)' probably refers to this specimen. Other examples of the species in old collections are variously labelled '*puzosianus*', '*bucklandi*', '*capricornu*', etc. The specific name '*bicarinatus*' alludes to the small ventro-lateral tubercles.

A. bicarinatum is the commonest species of *Aegocrioceras* in Bed C7G, and occurs also in the overlying Bed C7F. Usually only pyritized, septate inner whorl fragments are preserved, and the largest known specimen is an incomplete body chamber of an individual of about 100 mm estimated diameter. There is some variation in rib density, height of whorl, width of venter between the tubercles, strength of the tubercles and disposition of ribs; the neotype is towards one extreme, especially in possessing rectiradiate rather than prorsiradiate ribs. All variants differ from comparable growth stages of *A. semicinctum* in having a subquadrate instead of a rounded whorl section, and in lacking the mid-lateral tubercles distinctive of juvenile whorls of the latter species.

The inner whorls of *A. quadratum* are almost identical with *A. bicarinatum* in ratio of whorl thickness to whorl height, but these characters increase more rapidly in *A. quadratum*, the whorls remain almost in contact (compare Pl. 1, figs 1, 2) and

the ventro-lateral tubercles disappear at a relatively early growth-stage, so that the ventro-lateral region appears gently rounded rather than angular. In addition, the ribs of *A. quadratum* become gently flexuous during growth, while those of *A. bicarinatum* merely develop a forward bend high on the flank (cf. Pl. 1, figs 1, 2).

Pavlov's (1892) figured specimen of '*Crioceras*' *capricornu*, refigured by Wright (1957: L209; fig. 237, 3a, b) as *A. capricornu* (Roemer), belonged to *A. bicarinatum*: the specimen (formerly in the British Museum (Natural History) but now decomposed) was referred to by Koenen (1902: 320) who noted that it differed from the true *A. capricornu* in its more rounded cross-section, denser ribbing and more rapid increase in whorl thickness.

A. subseeleyi Spath is regarded as a junior subjective synonym of *A. bicarinatum*. The lectotype of Spath's species (Rawson 1970: 587) is refigured here (Pl. 2, fig. 1); it was identified by Dr A. von Koenen as '*Crioceras matheroni*' and so recorded by Danford (1906: 113). It differs from typical *A. bicarinatum* in having strongly prorsiradiate, more widely spaced ribs and a more compressed whorl, but extreme variants of *A. bicarinatum* show one or another of these features. One of the original syntypes of *A. subseeleyi*, the specimen figured by Phillips (1829: pl. 1, fig. 21) as '*Ancyloceras alternatus* Sowerby', can only questionably be attached to *A. bicarinatum* because of its small size.

DISTRIBUTION. Speeton, Heligoland, north Germany.

Aegocrioceras quadratum (Crick)

Pl. 1, figs 1, 3, 4; Pl. 2, fig. 2; Pl. 3, fig. 1; Text-fig. 1

- | | | |
|----|------|---|
| v* | 1898 | <i>Crioceras quadratum</i> (Bean MS) Crick: 74, 79, pl. 17, figs 10-13. |
| v | 1902 | <i>Crioceras torulosum</i> Koenen: 320, pl. 15, figs 4, 5. |
| v* | 1968 | <i>Aegocrioceras quadratum</i> (Crick) Jordan: 50. |
| v* | 1970 | <i>Aegocrioceras quadratum</i> (Crick); Rawson: 585, figs 1, 2. |

TYPE. BM. 89102 (Bean collection), from the Speeton Clay of Speeton, was designated lectotype and figured by Rawson (1970).

MATERIAL. 69 specimens (author's collection) from Speeton, mainly body chamber fragments: 1 almost complete specimen (BM. C78996), 59 body chambers (BM. C78997-79033; HU.Rn. 356-360, 1243-1245, 1329-1336, 1407-1409, 1440-1442) and 1 septate inner whorl (BM. C79034) from Bed C7F; 5 body chambers (BM. C79035-39) and 3 septate inner whorls (BM. C79040-42) from Bed C7G. 1 specimen from north Germany: GPiG. (uncatalogued).

DESCRIPTION. The whorl height increases moderately quickly so that the whorls remain almost in contact throughout growth. The whorl section is quadrate or subquadrate, the whorl flanks almost flat, either parallel or converging towards the venter. The venter is gently rounded, the dorsum flat or slightly concave (impressed), with slightly angular dorso-lateral region. The ribs are single, strong, initially straight and feebly prorsiradiate, becoming gently flexuous above about 40 mm diameter and remaining so to the adult body chamber. The ribs are usually

rectiradiate in general course on these whorls. At first, the ribs bear small ventro-lateral tubercles, stronger ones alternating with weaker, but these soon disappear and above about 20 mm diameter the venter becomes gently rounded.

Dorsal muscle scars are visible on some specimens (BM. C79001, C79010, C79013, 89102, C7154); they consist of two approximately semicircular smooth areas bounded by a shallow groove, and lie immediately anterior to the last septum.

DIMENSIONS of figured specimens :

BM. C79040 (Pl. 1, fig. 1). 57.8 : 21.3, 19.3(e), 26.0, 11.1(e). 41(e) ribs.

BM. C79041 (Pl. 1, fig. 3). 51.1 : 16.7, 16.5, 23.9, —.

DISCUSSION. The lectotype bears William Bean's original label '*Crioceratites quadratus*', a name finally published by Crick (1898). It consists of nearly half a whorl of body chamber with maximum whorl height 51.3 mm and thickness 43.4 mm. The ratio wt/wh is 0.85. Comparable body chambers, though normally with somewhat more inflated section (mean $wt/wh = 0.92$), are abundant in Bed C7F and reach a reasonably constant size (estimated diameters of 120–150 mm), which suggests that they are adult even though few show clearly adult features. This reflects the fact that the last few septa and the aperture are rarely preserved : occasionally the last few preserved ribs are closer together and less coarse.

The mean wt/wh is extremely close to that of the much smaller specimens of *A. bicarinatum* (0.91). However, the association of body chambers and inner whorls in 2 specimens of *A. quadratum* (e.g. Pl. 1, fig. 4) has allowed comparison with a few smaller, septate specimens (Pl. 1, figs 1, 3) which differ from *A. bicarinatum* in being more tightly coiled, with more flexuous ribs and less well-developed ventro-lateral tubercles. At all growth-stages, *A. semicinctum* has a more rounded whorl section than *A. quadratum*, and less numerous, slightly less flexuous ribs.

A. quadratum is quite common in north Germany, where it has usually been recorded as *A. torulosum* (Koenen). There is no significant difference between the syntypes of Koenen's species¹ and the lectotype of *A. quadratum*, so that *A. torulosum* is here regarded as a junior subjective synonym of *A. quadratum*.

DISTRIBUTION. Speeton, Heligoland, north Germany.

Aegocrioceras semicinctum (Roemer)

Pl. 2, fig. 3 ; Pl. 3, figs 2, 3

- | | | |
|---|--------|---|
| d | ? 1829 | <i>Hamites maximus</i> Sowerby ; Phillips : pl. 1, fig. 20 (<i>non</i> fig. 21). (2nd edit. 1835, 3rd edit. 1875). |
| | 1841 | <i>Hamites semicinctus</i> Roemer : 92, pl. 15, fig. 3. |
| v | 1902 | <i>Crioceras semicinctum</i> (Roemer) Koenen : 322, pl. 15, fig. 1. |
| v | 1970 | <i>Aegocrioceras semicinctum</i> (Roemer) Rawson : 591. |
| v | 1970 | <i>Aegocrioceras ligatum</i> (Bean MS) ; Rawson : 591. |

TYPE. One syntype, the Speeton Clay specimen figured by Phillips (1829 : pl. 1, fig. 20) as '*Hamites maximus* Sowerby', is lost ; the Heligoland specimen figured by

¹ The original of Koenen 1902 : pl. 15, fig. 5 is here designated lectotyp $\check{c}$ of *Aegocrioceras torulosum* (Koenen).

Roemer may still exist though it has not yet been traced. The species is interpretable from Roemer's description and figure, but will not be stabilized by designation of a lectotype or neotype until further enquiries have been made about the missing syntype.

MATERIAL. 21 specimens. In the author's collection 3 fairly complete specimens (BM. C78950-52) and 11 body chambers (BM. C78953-59; HU.Rn. 105, 676, 823, 1186) from Bed C7F; 2 inner whorl fragments (BM. C78960-61) from Bed C7G. In other collections 5 almost complete specimens in nodules of Bed C7F type: GSM. 17495, 22226 (Danford collection); SM. B53171; YM. 885, PR/1975/1 (Bean collection); Wrights' collection 21849.

DESCRIPTION. The shell is fairly tightly coiled, the whorl height increasing moderately rapidly; the whorl section is almost circular but slightly higher than wide ($wl/wh = 0.96$). The dorsum is flat, the dorso-lateral edge and flanks rounded, the venter flat on inner whorls becoming more rounded with growth. The strong, single, radial ribs are initially straight and rectiradiate: later they become rursiradiate and may be slightly flexuous. The inner whorls bear small ventro-lateral tubercles on most ribs; these gradually diminish and eventually disappear at diameters of 40-50 mm. In the earliest whorls occasional tubercles are more strongly developed, and up to about 25-30 mm diameter mid-lateral and sometimes dorso-lateral tubercles occur on some ribs.

Muscle scar impressions are preserved on one specimen (HU. Rn.105); they are like those of *A. quadratum*.

DIMENSIONS of figured specimens:

GSM. 22226 (Pl. 2, fig. 3). 86.1: 30.3(e), 29.8, 42.4(e), 4.0(e). 46 ribs.

YM. 885 (Pl. 3, fig. 3). 75.3: 25.2, -, 34.2, 3.3. 41 ribs.

DISCUSSION. At Speeton, *A. semicinctum* is represented mainly by body chamber fragments, but several specimens have earlier whorls preserved. Although definite adult characters are difficult to distinguish, the relatively constant size of body chambers from the same nodule band (in C7F) that also yields consistently larger body chambers of *A. quadratum* suggests that *A. semicinctum* generally grew to a diameter of about 100-120 mm.

There is some variation in whorl proportions and degree of uncoiling, but none of the variants is as tightly coiled as *A. quadratum*. *A. semicinctum* differs from other species in its inflated, subcircular whorl section and in having mid-lateral tubercles in the inner whorls. Body chambers are distinguished from those of *A. quadratum* by their less flexuous, stronger, rursiradiate ribs and rounded instead of subquadrate whorl section, though a few specimens appear intermediate in form and are difficult to distinguish.

William Bean applied his manuscript name '*Crioceratites ligatus*' to *A. semicinctum*: in addition to the York Museum specimen (Pl. 3, fig. 3) previously recorded as bearing a Bean label (Rawson 1970: 591) there is another specimen at York. A third example (Bean collection, BM. 89101) is of an indeterminate species. Subsequent collectors applied the name indiscriminately.

DISTRIBUTION. Speeton, Heligoland, north Germany.

Aegocrioceras raricostatum (Phillips)

Fig. 1c.; Pl. 4, figs 6-10; Pl. 5, figs 3, 4, 7

- d* 1829 *Hamites raricostatus* Phillips: pl. 1, fig. 23 (2nd edit. 1835, 3rd edit. 1875).
 d non 1841 *Hamites raricostatus* Phillips; Roemer: 93, pl. 13, fig. 14.
 d ? 1902 *Hamites raricostatus* Phillips; Koenen: 320.
 v 1902 *Hamites intermedius* Phillips (*non* Sowerby); Koenen: 319.
 v 1906 *Hamites intermedius* Phillips; Koenen *in* Danford: 114.
 v 1924 *Aegocrioceras intermedium* (Phillips) Spath: 76, 77.
 v 1924 *Toxoceratoides rotundus* Bean MS *non* Phillips; Spath: 78.
 v 1970 *Aegocrioceras* sp. nov. Rawson: 589.
 v 1971b *Aegocrioceras* sp. nov. Rawson 1970; Rawson: 70.

TYPE. The holotype, originally in the Williamson collection in Scarborough Museum, is lost; BM. C78963 (author's collection), from Bed C7D of the Speeton Clay, is here designated neotype.

MATERIAL. 44 specimens from Speeton and 3 from north Germany. Speeton: (author's collection) BM. C78964-72 from Bed C7D; HU.Rn. 99, 874, 941, 942 (no horizon); (other collections) HU. Neale collection S943, S1526-28, S1530; HM. 22/64/12; BM. C72669, C78973, C72671 (Lamplugh collection), 89106 (Bean collection), C78962 (Kelly collection); GSM. 17449, 17480, 17482-7, 17489, 17490, 17492, 17502 (all Danford collection), 32137, 32140, 32151 (Marchioness of Hastings collection), 32135; SM. B53164 (Leckenby collection), 53148; Wrights' collection 10386, 20392. North Germany: NLFb. Kh.67; GPIG. (two uncatalogued specimens).

DESCRIPTION. The whorl height is low in relation to diameter and increases very slowly; adjacent whorls are well separated. The whorl is moderately compressed ($wt/wh = 0.74$) with flat or gently curved flanks and subrectangular to oval section; the ventro-lateral and dorso-lateral edges are rounded and merge into the flanks except in specimens less than about 10 mm diameter where small ventro-lateral tubercles impart a slight angularity to this region. The dorsum varies from almost flat to convex. The ribs are strong, simple and widely spaced; on the whorl flanks they are slightly prorsiradiate in general course but convex forwards, usually curving gently backwards near and over the venter. The dorsum bears well-developed, though small, forwardly curving rib-folds. The septa are well spaced, and individual lobes and saddles not very deeply subdivided (Fig. 1c), so that adjacent sutures are clearly separated from one another throughout their length.

DISCUSSION. Phillips (1829, 1835, 1875) did not describe the species and his figure was sketchy; as the holotype is lost both Howarth (1962: 129) and the author (Rawson 1970: 590) have regarded *A. raricostatum* as uninterpretable. However, among the numerous whorl fragments now attributed to this species several agree fairly closely with Phillips' figure in having widely spaced ribs, and the 2 specimens in the Wrights' collection (e.g. Pl. 5, fig. 3) are an almost perfect match. All exhibit the gentle shell curvature which is also indicated by Phillips' figure, and in some specimens the ribs also thicken towards the venter exactly as he indicated. The sparsely ribbed forms such as the holotype are clearly an extreme form of a

variable assemblage whose more typical, relatively closely ribbed members include the specimens (e.g. GSM. 17484-7) which Koenen (1902), Danford (1906) and Spath (1924) recorded as *A. intermedium* 'Phillips' and Rawson (1970) described as *A.* sp. nov. The specimen now selected as neotype of *A. varicostatum* is intermediate between these and Phillips' holotype in rib density; its maximum whorl height is about the same as the minimum height on Phillips' illustration.

In addition to this variation in rib density, there is some in whorl proportions. This is particularly apparent in the juvenile whorls, where forms with a more rounded whorl and relatively low height exemplify a very distinct variant. A small specimen in the Bean collection (BM. 89106: Pl. 4, fig. 7) bears Bean's original label '*Hamites rotundus* Phillips', while a larger one in the Lamplugh collection (BM. C72671: Pl. 4, fig. 10) bears a modern label '*Toxoceratoides rotundus* Bean MS non Phillips' which Mr D. Phillips informs me was probably copied from an earlier Spath label: these are presumably the originals of Spath's record of *T. rotundus* (Bean MS non Phillips) from the Upper B Beds. The Lamplugh specimen has an associated, but loose, label recording it from the B Beds. In fact, both specimens are extremely close to a fragment of intermediate size from Bed C7D (Pl. 4, fig. 9) which has a *wt/wh* ratio of 0.90, compared with a mean ratio 0.74 for the typical compressed forms of *A. varicostatum*.

Nearly all the specimens of *A. varicostatum* consist of short fragments, and specimens of more than half a whorl are rare at Speeton. The curvature of these bigger pieces is usually slightly irregular, but this is probably a result of post-depositional deformation, for regular curvature is apparent in some north German examples. The latter include fragments indicating that the species attained a diameter of at least 200 mm.

A. varicostatum is most closely approached in rib style and density by *A. spathi*, and both species were labelled '*varicostatum*' by the early collectors. However, *A. varicostatum* is distinguished from this and other *Aegocrioceras* by the loosely coiled, gently curved shell and very slow increase in whorl height. The septa are more widely spaced and the elements of the suture shorter and less deeply subdivided than in other species. The Heligoland specimen figured by Roemer (1841) as *Hamites varicostatus* apparently had ventro-lateral tubercles and does not therefore agree with the Speeton forms.

DISTRIBUTION. Speeton, Heligoland (Rawson 1974), north Germany.

Aegocrioceras compressum sp. nov.

Pl. 5, figs 2, 6

v 1971b *Aegocrioceras* sp. a. Rawson: 70.

DIAGNOSIS. A very compressed species with feebly convex ribs which curve slightly backwards over the venter. Some ribs are intercalated low on the whorl flank and a few stand out more sharply than the rest.

HOLOTYPE. BM. C78974 (author's collection) from Bed C7D of the Speeton Clay, Speeton.

PARATYPES. 5 whorl fragments, all collected by the author. BM. C78975-6 from Bed C7E, Speeton; BM. C78977 (no horizon), Speeton; NLfB. Kh.68, 69 from the *Aegocrioceras* Zone at Ovenstadt, near Petershagen, north Germany.

DESCRIPTION. The whorl height increases moderately quickly and the whorls are probably fairly tightly coiled. The shell is compressed ($wt/wh = 0.67$) with flat flanks, gently rounded venter and nearly flat dorsum. The ribs are single, almost straight at first but soon becoming slightly convex towards the aperture and curving gently backwards over the venter. Initially the ribs are of equal strength and bear feeble ventro-lateral tubercles; the tubercles disappear by about 10 mm diameter, while above about 20 mm diameter some ribs stand out slightly more sharply than the rest and a few of the intervening ribs are intercalated low on the whorl flanks instead of appearing at the umbilical edge. Most of those ribs which extend down to the umbilical edge form strong, forwardly curving folds on the dorsum.

DIMENSIONS of figured specimen :

BM. C78974 (Pl. 5, fig. 2). 41.1 : 13.4, 8.9, 19.4, -.

DISCUSSION. The various whorl fragments assigned to this species, of which the holotype is the most complete, represent growth stages to an estimated diameter of 150 mm. All are distinguished from other *Aegocrioceras* by the occurrence of occasional slightly stronger ribs and the very compressed shell. *A. densiradiatum* approaches *A. compressum* in the compression of the shell ($wt/wh = 0.71$) and in the occurrence of occasional intercalated ribs, but has more numerous, finer ribs of approximately equal strength.

DISTRIBUTION. Speeton, north Germany.

Aegocrioceras spathi sp. nov.

Pl. 4, figs 1, 2, 5

d ? 1881 *Crioceras* n. f. cf. *capricornu* Roemer; Neumayr & Uhlig : 67, pl. 53, fig. 5.
v 1971b *Aegocrioceras* sp. b Rawson : 70.

DIAGNOSIS. A fairly compressed species ($wt/wh = 0.78$) in which the whorl height increases moderately quickly in relation to diameter. The ribs are convex forwards on the whorl flank and curve gently backwards over the venter.

HOLOTYPE. BM. C78978 (author's collection) from the Speeton Clay. The specimen was not found *in situ* but is in a red siltstone matrix which matches Bed C7A, from which 3 paratypes have been collected.

PARATYPES. 19 specimens from Speeton and 3 from north Germany. Speeton : (author's collection) BM. C78979-84 from Bed C7B, C78985 from C7A; HU.Rn. 117, 633 from Bed C7A; HU.Rn. 399, 938 horizons not known. (Other collections) BM. 89100 (Bean collection); C72668 (Lamplugh collection); GSM. 17496 (Danford collection); Wrights' collection 6297-9; YM. PR/1975/2-3. North Germany : NLfB. Kh.66 (author's collection) from Sarstedt; GPIG. (two uncatalogued specimens) from Schulenburg.

DESCRIPTION. The whorl height increases moderately quickly though the whorls remain well separated. The shell is moderately compressed with subrectangular whorl section ($wt/wh = 0.78$); the flanks are almost flat, the venter gently rounded and the dorsum flat. The ventro-lateral region is rounded except in the earliest growth stages (to about 10 mm diameter) where small tubercles occur. The ribs are single, strong, slightly convex towards the aperture on the flanks and curving gently backwards over the venter. They are rectiradiate or prorsiradiate in general course. In early growth stages the dorsum is crossed by feeble rib-folds and growth striae, which curve gently forwards; on later whorls it is crossed by growth striae only. The number of ribs increases gradually with growth, from about 33 at 14 mm diameter (BM. C78980) to 35 at 45 mm (NlfB. Kh.66) and 44 at 67 mm diameter (BM. 89100).

DIMENSIONS of figured specimen:

BM. C78978 (Holotype: Pl. 4, fig. 2). 52.3. At 47.9: 14.5, 10.5, 25.0(e), -. Approx. 35 ribs.

The figured paratypes are slightly crushed or distorted.

DISCUSSION. *A. spathi* shows slight variation in both the rapidity with which the whorl height increases and in degree of curvature of the ribs. Several specimens have at least one complete whorl preserved; of these, the holotype, BM. C72668, BM. C89100 and YM. PR/1975/2 are preserved in a red siltstone matrix which matches the lithology of the prominent siltstone Bed C7A, from which 3 other specimens were collected. BM. C89100 was collected by William Bean and bears his original label '*Crioceratites varicostatus*'. It is the largest known Speeton specimen of *A. spathi* and has a diameter of about 93 mm, but fragments of much larger individuals of *A. cf. spathi* from north Germany (author's collection) indicate that the species probably grew to at least 300 mm diameter.

A. spathi is slightly more coarsely ribbed than *A. varicostatum*, the whorls are less well separated, the whorl height expands more rapidly and the dorsum is flatter. *A. capricornu* has relatively straight, sharper, more numerous ribs and the whorls are a little more inflated and much closer together than those of *A. spathi*. *A. compressum* is more compressed and has less regular, denser ribbing. The specimen from Egistorf figured by Neumayr & Uhlig (1881) is probably a variety of *A. spathi* with almost straight, slightly more closely spaced ribs.

DISTRIBUTION. Speeton, Heligoland (Rawson 1974), north Germany.

Aegocrioceras densiradiatum Rawson

Pl. 6, fig. 2

- | | | |
|----|------|---|
| v | 1906 | <i>Crioceras puzosianum</i> ? d'Orb; Koenen in Danford: 113. |
| v | 1924 | <i>Aegocrioceras</i> sp. nov. aff. <i>capitanei</i> (Bean MS); Spath: 77. |
| v* | 1970 | <i>Aegocrioceras densiradiatum</i> Rawson: 589, figs 8-10. |

TYPE. The holotype, BM. C72704 (Bean collection) from the Speeton Clay of Speeton, is refigured here (Pl. 6, fig. 2).

MATERIAL. In addition to the holotype and 4 paratypes (BM. C75710 ; GSM. 17498, 32125-6), there are 3 additional specimens from Speeton : BM. C78986-87 (author's collection), horizon not known ; GSM. 17479 (Danford collection).

DISCUSSION. The exact horizon of this species is still not known, but the Danford collection specimens are labelled 'Zone C' (GSM. 17498) and 'C6' (GSM. 17479). Specimens BM. C78986-87 (author's collection) were picked up on the lower part of the weathered slopes of Middle Cliff, where Beds C5-7 crop out. A middle C Beds horizon for this form would negate a tentative suggestion (Rawson 1970 : 589) that it may have given rise to *Hoplocrioceras phillipsi* (Phillips), since the latter probably occurs much higher, in the upper part of the Lower B Beds (Rawson 1975).

A. densiradiatum is distinguished from all other species of *Aegocrioceras* by its fine, dense ribs. In general whorl proportions it is most closely approached by *A. capricornu* and *A. compressum*, and, like the latter, *A. densiradiatum* has very occasional intercalated ribs. However, *A. compressum* has intermittent stronger ribs and a slightly more compressed whorl section.

DISTRIBUTION. Speeton.

Aegocrioceras capricornu (Roemer)

Pl. 5, fig. 1

d* 1841 *Hamites capricornu* Roemer : 92, pl. 14, fig. 6.

DISCUSSION. Although this is the most frequently quoted species in the German literature, it remains difficult to interpret. Roemer's (1841) figured 'syntype' (possibly two specimens) is lost ; it is this Heligoland specimen that was relied upon by subsequent German workers for the interpretation of the species. However, Roemer also referred Phillips' (1829 : pl. 1, fig. 22) figured '*Hamites intermedius*' to *A. capricornu*, and this is therefore another syntype. Phillips' specimen is also probably lost, for the partially decomposed specimen in the Yorkshire Museum (YM. 419A) labelled as his original does not match the figure at all closely. *A. capricornu* is best stabilized by selection of a neotype that will conform with German palaeontologists' usage. Neumayr & Uhlig (1881 : 194) probably interpreted the species correctly, though their figured specimens were all larger than Roemer's (1841) Heligoland original(s). Two fragmentary specimens (Neumayr & Uhlig 1881 : pl. 53, figs 6, 7) from the Schloenbach collection are in the Zentrales Geologisches Institut, Berlin, and have been loaned to me through Dr Vogel. One (fig. 6) is an internal mould, while the other has shell preserved and is a slightly less inflated form. The most complete individual (pl. 53, fig. 4), from the Strombeck collection, is lost.

A. capricornu is characterized by whorls which, though uncoiled, are almost in contact (Neumayr & Uhlig 1881 : pl. 53, fig. 4). The whorl is higher than wide, with subquadrate whorl section and flat flanks (Roemer 1841 : 92). The strong radial ribs are straight or feebly prorsiradiate, at least in the earlier whorls, being prominent and sharp where the shell is preserved but more rounded and distinctly broader and flatter over the venter in internal moulds. Whorl fragments with this style of ribbing are common in the German *Aegocrioceras* Zone, but more complete

specimens are rarely found and are poorly represented in the museum collections. A specimen from Osterwald, near Hanover, figured here (Pl. 5, fig. 1) as *A. capricornu*, differs from Neumayr & Uhlig's figured specimens only in the change from straight, rectiradiate ribs in the inner whorls to slightly curved, rursiradiate ribs above about 60 mm diameter. This more advanced rib pattern approaches that of some much larger individuals from the *Aegocrioceras* Zone of Hildesheim which Koenen (1902: pl. 16, figs 1-4) figured as *A. capricornu*.

None of the Speeton *Aegocrioceras* can be identified as *A. capricornu*. With the exception of *A. quadratum*, all have more widely separated whorls. The whorl height of *A. capricornu* increases less rapidly than that of *A. quadratum*, and in whorl proportions *A. capricornu* is between that species and the more compressed group of *A. spathi* and *A. raricostatum*. The ribs of the last two species are convex forwards on the flanks and curve gently backwards over the venter, where they remain narrow and sharp even on internal moulds. In general morphology *A. capricornu* therefore lies between the early *Aegocrioceras* of the *quadratum* group and the younger, more compressed forms; it is provisionally inserted in this position in Fig. 3 (p. 151).

DISTRIBUTION. North Germany.

Aegocrioceras ? *seeleyi* (Neumayr & Uhlig)

Pl. 6, fig. 1

- 1881 *Crioceras seeleyi* Neumayr & Uhlig: 54, pls 51, 52.
 1902 *Crioceras* cf. *seeleyi* Neumayr & Uhlig; Koenen: 280.
 1904 *Crioceras seeleyi* ? Neumayr & Uhlig; Koenen: 42.

MATERIAL. 4 whorl fragments from Speeton, 1 from Flamborough. BM. C78988-89 (author's collection) from Bed C4L, Speeton; HU. Neale collection S.705, S.1507 from Speeton; BM. C78990 (collected by Mr M. Howgate) from the Speeton Clay erratic at Flamborough Head.

DISCUSSION. The German specimens figured by Neumayr & Uhlig (1881), though variable, all apparently belong to one species characterized by a subquadrate whorl section and slightly flexuous ribs of which occasional ones are slightly stronger and bear well-developed ventro-lateral tubercles, sometimes with feeble dorso-lateral and even mid-lateral tubercles: the Speeton fragments fit well within the range of variation of the north German examples that I have examined. Because of the slightly stronger ribs and the well-developed tubercles, both *A. seeleyi* and *A. koeneni* (described below) are difficult to assign to a genus. Although they stand apart from typical *Aegocrioceras* they also lack the periodic well-defined, strong, bi- or trituberculate ribs of *Crioceratites*. It is, therefore, hardly surprising that Spath (1924: 84) regarded '*Crioceras*' *seeleyi* as a transitional link between *Aegocrioceras* and *Crioceratites*, while including both this species and *A. ? koeneni* in *Aegocrioceras*. However, there is a stratigraphical gap between the *Aegocrioceras* fauna of Bed C7 and *A. ? seeleyi*, typical *Crioceratites* occurring both with and between the two, so

that the 'transitional' nature of *A. ? seeleyi* may be fortuitous. Its exact origin remains obscure, but it could be an offshoot from contemporaneous *Crioceratites* rather than from earlier *Aegocrioceras*.

The inner whorls of *A. ? seeleyi* have never been described, and I have failed to find associated outer and inner whorls either in the field or in German or English museums. Circumstantial evidence suggests that *A. ? koeneni* may represent these inner whorls : in addition to their morphological similarity, the two species occur together in north Germany, where I have collected them from a horizon in the *ihmensis* Subzone about 9 m above the *Aegocrioceras* Zone at Ziegelei Moorberg, Sarstedt. Mr M. Howgate has collected fragments of both species from the Speeton Clay erratic at Flamborough Head described by Kendall & Wroot (1924 : 788). At Speeton, *A. ? seeleyi* occurs in Bed C4L with the zonal fossil *Simbirskites* (*Craspedodiscus*) *gottschei* (Koenen) but the horizon of *A. ? koeneni* is not known.

DISTRIBUTION. Speeton, Flamborough, Heligoland, north Germany.

Aegocrioceras ? koeneni Spath

Pl. 4, figs 3, 4 ; Pl. 5, fig. 5

- d* 1829 *Hamites maximus* Sowerby ; Phillips : 123, pl. 1, fig. 21 (*non* fig. 20). (2nd edit. 1835).
d* 1875 *Ancyloceras grande* (Forbes) Judd ; Phillips : 274, pl. 1, fig. 21 (*non* fig. 20).
d* 1924 *Aegocrioceras koeneni* Spath : 77.
v 1969 *Aegocrioceras koeneni* Spath ; Hiltermann & Kemper : 23, pl. 2, fig. 7.
v 1970 *Aegocrioceras koeneni* Spath ; Rawson : 587, figs 6, 7.

TYPE. The neotype, HU. Neale collection S.1731, from the Speeton Clay of Speeton, was designated by Rawson (1970) and is refigured here, Pl. 4, fig. 3.

MATERIAL. 10 whorl fragments from Speeton (exact horizons not known) : BM. C78991-94 (author's collection), C72171 (W. T. Dean collection) ; HM. 22/64/13 ; HU. Neale collection S.576, S.1516, S.1521 ; Wrights' collection 19053. 1 small fragment from the Speeton Clay erratic, Flamborough Head, BM. C78995 (collected by Mr M. Howgate).

DESCRIPTION. The species is only known from septate whorl fragments of specimens up to about 50 mm diameter. The shell is moderately compressed with subquadrate whorl section and flat flanks. The dorsum is flat or slightly concave, crossed by forwardly curving rib-folds. The ribs are strong, simple, straight and rectiradiate or gently prorsiradiate on the lower part of the flank but curving forward more strongly nearer the venter. The ribs thicken towards and on the narrow venter, where some are raised slightly higher than the rest. Most ribs swell feebly at the ventro-lateral edge, which thus appears angular.

DISCUSSION. The strong forward curvature of the ribs near the venter and the increase in height and thickness of some ribs in the ventral region distinguish *A. ? koeneni* from the comparable growth stages of all other *Aegocrioceras*. The largest specimen known (Pl. 4, fig. 4) is only about 50 mm in diameter, but more advanced growth stages of this species may be represented by *A. ? seeleyi*.

DISTRIBUTION. Speeton, Flamborough, Heligoland, north Germany.

Other available specific names

Aegocrioceras bucklandi (Buckland). Buckland's (1836: 65, pl. 44, fig. 1) figure indicates a rib curvature and degree of uncoiling reminiscent of *A. spathi* or *A. raricostatum*; the holotype could, however, be the same specimen which Phillips (1829) had earlier figured as *Hamites intermedius* (Sowerby) (Rawson 1970: 590) and which is also a syntype of *Hamites capricornu* Roemer 1841. Fragments of a partially decomposed specimen in the Yorkshire Museum (tablet 419A) are labelled as Phillips' original, though the attribution is doubtful (see also p. 147). This specimen is closest to some of the extremes of *A. bicarinatum*, to which species the name '*bucklandi*' was often applied by early collectors (e.g. Marchioness of Hastings collection). In view of all the problems of interpretation attached to Buckland's species, the name '*Hamites bucklandi*' should fall into disuse.

Aegocrioceras subnodosum (Roemer). Roemer's (1841: 93, pl. 13, fig. 10) figured '*Hamites subnodosus*' is a short whorl fragment of an indeterminate *Aegocrioceras*. From his figure and brief description it could be an example of *A. bicarinatum* (Young & Bird 1828). Roemer's specific name has been little used by subsequent workers, though it was listed by Spath (1924).

V. THE SUCCESSION OF SPECIES IN THE SPEETON CLAY

Species subsequently assigned to *Aegocrioceras* have long been known to characterize a narrowly defined horizon (Bed C7) at Speeton (e.g. Leckenby 1859; Judd 1868; Lamplugh 1889), which Spath (1924) attempted to subdivide by proposing the zones of *A. capricornu* and *A. capitanei*, the former underlain by an unnamed horizon. *A. capitanei* is a Bean manuscript name based on an indeterminate fragment (Rawson 1970: 591), and it is not clear which of the species described above in section IV is the intended index of the '*capricornu* Zone', though most of the specimens which Spath identified as *A. capricornu* belong to *A. bicarinatum*. For these reasons I have abandoned Spath's scheme and placed the whole of Bed C7 in the *Simbirskites* (*Speetonicer*) *inversum* Zone (Rawson 1971a, 1971b). *Aegocrioceras* appears suddenly, and in abundance, in Bed C7G, about 0.3 m above the first appearance of *S. (Sp.) inversum*, and remains the dominant ammonite through the rest of C7. A *Speetonicer* was chosen as zonal index because, despite the abundance of *Aegocrioceras*, the appearance of the latter genus represents a short-lived incursion into a region generally dominated by *Simbirskites* (Rawson 1973: fig. 4). Two discrete *Aegocrioceras* assemblages were noted, a lower one of relatively inflated species in Beds C7G and C7F, followed by a group of more compressed forms in C7E-C7A (Rawson 1971b: 70). The difference in whorl section of the two groups is brought out by the break between species with a mean *wt/wh* ratio of 0.96-0.91 and those with mean ratio 0.78-0.67 (Table 1, p. 134).

The range and relative abundance of *Aegocrioceras* species in Bed C7 is summarized in Fig. 2. This clearly shows that the younger of the two assemblages previously recorded can be split, so that a total of three assemblages may be recognized. Although they are of clear stratigraphical significance they are not given the status of subzones here, since the faunal sequence is probably condensed and incomplete (see below).

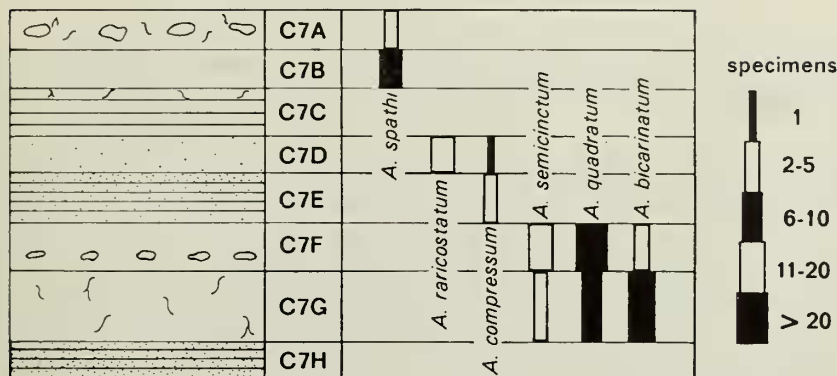


FIG. 2. Range and abundance of *Aegocrioceras* species in Bed C7, Speeton.

Assemblage 1 consists of the relatively stout-whorled species *A. semicinctum*, *A. quadratum* and *A. bicarinatum*, and is confined to Beds C7G and C7F.

Assemblage 2 contains *A. varicostatum* and *A. compressum*, though the former species is the dominant form. Both are considerably more compressed than members of *Assemblage 1*. *Assemblage 2* is confined to Beds C7E and C7D.

Assemblage 3 consists of a single species, *A. spathi*, which occurs in Beds C7B and C7A (Bed C7C has not yielded *Aegocrioceras*). The first *Crioceratiles* appear with late *A. spathi* in Bed C7A.

The rapid changes in distinct faunal assemblages through only 2.6 m of clay suggest a very condensed sedimentary sequence. This is also indicated by lithological evidence: *Chondrites* burrows, abundant glauconite (C7E), rapid colour changes and the occurrence of partially phosphatized nodules (in C7F and C7A) are all characteristic of interrupted or slow deposition. Furthermore, the equivalent beds are often much expanded in thickness in the Lower Saxony Basin in north Germany.

The relatively condensed nature of the Speeton succession implies that the preserved fauna may not reflect the whole spectrum of *Aegocrioceras* forms; *A. capricornu* is certainly absent. This makes it difficult to postulate an evolutionary lineage, though a possible one is summarized in Fig. 3. The lineage requires testing by further work on the north German faunas.

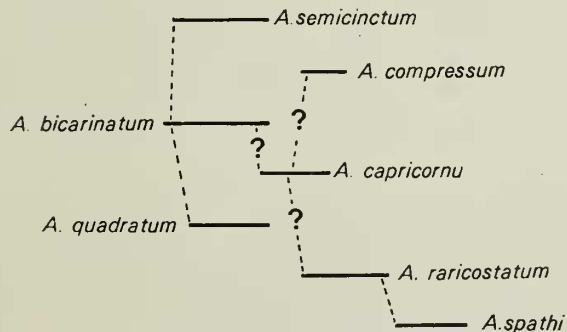


FIG. 3. Possible evolutionary lineages in *Aegocrioceras*.

VI. COMPARISON WITH OTHER AEGOCRIOCERAS FAUNAS

Aegocrioceras faunas are known from two other regions, the North Sea island of Heligoland and the Lower Saxony Basin of the north German mainland.

Heligoland. Lower Cretaceous clays crop out on the sea floor east of the main island ('Hauptinsel') of Heligoland, and ammonites washed up on the northern shore of the adjacent islet of Düne were first described by Roemer (1841). Heligoland and Speeton are, jointly, type localities for three species proposed by Roemer and now attributed to *Aegocrioceras*, namely '*Hamites*' *semicinctus*, '*H.*' *capricornu* and '*H.*' *subnodosus*. Koenen (1904) added *A. torulosum* (Koenen 1902) [= *A. quadratum* Crick 1898] and *A. ? seeleyi* (Neumayr & Uhlig) to the Heligoland records, and Hiltermann & Kemper (1969) figured *A. bicarinatum* (Young & Bird) and *A. ? koeneni* Spath.

Recently, skin-divers have collected about 100 *Aegocrioceras* loose from the sea floor, along with many other Lower Cretaceous ammonites (Kemper *et al.* 1974). The *Aegocrioceras* fauna is discussed in detail elsewhere (Rawson in Kemper *et al.* 1974; Rawson 1974); in both species content and preservation it is remarkably similar to that of the Speeton Clay, even to *A. quadratum* and *A. semicinctum* occurring as partially phosphatized body chambers or in phosphatic nodules – the preservation characteristic of the same species in Bed C7F at Speeton.

The new collections confirm the occurrence of *A. quadratum*, *A. bicarinatum*, *A. semicinctum*, *A. ? koeneni* and *A. ? seeleyi*, and add *A. spathi* and *A. varicostatum* to previous records. Thus the only Speeton species not represented from Heligoland are *A. compressum* and *A. densiradiatum*.

The Lower Saxony Basin. The stratigraphy, palaeontology and regional distribution of Lower Cretaceous sediments in the Lower Saxony Basin are extensively reviewed by Thiermann & Arnold (1964), Schott *et al.* (1967, 1969) and Kemper (1973a, 1973b). Through much of the Lower Cretaceous clays accumulated in the main part of the basin, and the central basin facies consists mainly of dark, shaley clays with bands of red-weathering, ferruginous concretions. The shallower-water and marginal facies are more varied, with sandstones, limestones and ironstones developed.

The abundance of *Aegocrioceras*, especially in argillaceous sediments, led to the recognition of an *A. capricornu* Zone (Koenen 1902) which is customarily taken as the base of the German Upper Hauterivian. Riedel (*in* Gürich & Dacque 1942) attempted to subdivide the zone but his subdivisions are difficult to uphold (e.g. Zedler 1959) and recent authors have reverted to a simpler *capricornu* Zone. The definition of this has varied, some authors including in it beds with early *Simbirskites* (the 'Obere *capricornu*-Zone') above the main *Aegocrioceras* horizon. Kemper (1973a) has proposed the term '*Aegocrioceras* spp. Zone' for the limited *capricornu* Zone; this correlates with the vertical distribution of *Aegocrioceras* (excluding *A. ? seeleyi* and *A. ? koeneni*) at Speeton.

The rich fauna of the *Aegocrioceras* Zone has never been adequately described though some species were described and figured by Neumayr & Uhlig (1881) and Koenen (1902). The numerous specimens in museum collections indicate that all three Speeton assemblages occur, especially in some of the prolific temporary sections exposed during the digging of the Mittelland Canal (completed in 1938). At present, the zone is exposed *in situ* at Ovenstadt (near Petershagen) and Sarstedt (near Hanover).

At Ovenstadt, basin-facies shaley clays yield abundant, though usually fragmentary, specimens, often of large size. The *Aegocrioceras* Zone is at least 15 m thick here, but the *A. quadratum/bicarinatum/semicinctum* fauna of Assemblage 1 at Speeton has not been collected; it presumably lies beneath the lowest exposed horizon. There is an upward passage into the *Simbirskites (Milanowskia) staffi* Zone. Because of their large size, representing growth stages more advanced than those preserved at Speeton, most *Aegocrioceras* from this locality are difficult to compare with Speeton forms; the specimens in my collection are identified as *A. capricornu*, *A. cf. varicostatum*, *A. compressum* (Pl. 5, fig. 5) and *A. cf. spathi*, indicating Assemblages 2 and 3.

At Sarstedt, flattened *Aegocrioceras* (complete with shell) are abundant through about 3 m of clay, though three-dimensional specimens are rare. The latter are pyritized, with shell, and normally not more than about 50 mm in diameter, so that they can be compared directly with Speeton specimens. The earliest forms belong to *A. varicostatum*, representing Assemblage 2. This is replaced higher up by *A. spathi* (Pl. 4, fig. 5), which in turn gives way abruptly to *Simbirskites* of the *staffi* Zone (Rawson 1971a : 75). The absence of Assemblage 1 is puzzling, since there is no obvious stratigraphical break, but may be explained by preservation failure since the clays beneath the *Aegocrioceras* Zone are completely without ammonites for several metres.

The similarity in preservation of the Sarstedt and Speeton *Aegocrioceras* (and *Endemoceras* and *Simbirskites*) is mirrored by the lithological similarity, the clays at both localities being much more varied in colour and mineral content than the basin-facies sediments. The clays at Sarstedt were deposited in relatively shallow water on the flanks of a salt-stock.

At Gildehaus, near Bentheim, blocks of Gildehauser Sandstone from a temporary section have yielded flattened *Aegocrioceras* (see Kemper 1968 : pl. 3, fig. 2), among which I have identified *A. sp. cf. quadratum* (Kemper's figured specimen) and *A. varicostatum* (Bramer collection, author's collection).

VII. CONCLUSIONS

The main *Aegocrioceras* fauna of the Speeton Clay occurs in Bed C7, where three distinct assemblages can be recognized through only 2.6 m of clay. The sequence is condensed and may not represent the whole spectrum of *Aegocrioceras* species. Two further 'species', only provisionally retained in *Aegocrioceras*, probably occur together higher in the succession; one, *A. ? koeneni*, may be the inner whorls of the other, *A. ? seeleyi*.

All but one of the species recorded from Speeton occur in north Germany, and all but two are known from Heligoland.

Of the 12 specific names previously published for *Aegocrioceras* species, two are regarded as uninterpretable and two others as junior subjective synonyms. Another two species are newly described in this paper. A full list of previously published names and their interpretation is given in Table 3. Many unpublished names and misidentifications were listed by Spath (1924); these are tabulated in the Appendix (below).

TABLE 3

Previously published specific names in *Aegocrioceras*, and their present interpretation

Specific name	Interpretation in this paper
<i>bicarinatum</i> Young & Bird 1828	<i>bicarinatum</i> Young & Bird 1828
<i>bucklandi</i> Buckland 1836	uninterpretable
<i>capricornu</i> Roemer 1841	<i>capricornu</i> Roemer 1841
<i>densiradiatum</i> Rawson 1970	<i>densiradiatum</i> Rawson 1970
<i>koeneni</i> Spath 1924	<i>koeneni</i> Spath 1924 (? = <i>seeleyi</i> Neumayr & Uhlig 1881)
<i>quadratum</i> Crick 1898	<i>quadratum</i> Crick 1898
<i>ravicostatum</i> Phillips 1829	<i>ravicostatum</i> Phillips 1829
<i>seeleyi</i> Neumayr & Uhlig 1881	<i>seeleyi</i> Neumayr & Uhlig 1881
<i>semicinctum</i> Roemer 1841	<i>semicinctum</i> Roemer 1841
<i>subnodosum</i> Roemer 1841	uninterpretable (? <i>bicarinatum</i> Young & Bird)
<i>subseeleyi</i> Spath 1924	<i>bicarinatum</i> Young & Bird 1828
<i>torulosum</i> Koenen 1902	<i>quadratum</i> Crick 1898

VIII. APPENDIX: SPATH'S (1924) FAUNAL LIST

Dr L. F. Spath examined the collections 'of many Public Museums and numerous private collectors' (Spath 1924: 73) during the compilation of his exhaustive list of Speeton Clay ammonites: evidence within his paper shows that he saw collections in the British Museum (Natural History), the Geological Survey Museum (which already included the Danford collection), the Sedgwick Museum, Hull Museum, Scarborough Museum and the Yorkshire Museum, together with the private collection of G. W. Lamplugh now in the British Museum (Natural History). The Herries collection, subsequently transferred to the Yorkshire Museum, also bears some labels in Spath's handwriting, apparently predating his 1924 paper.

In attempting to list the whole of the Speeton Clay fauna Spath could not hope to provide a critical revision, so that it is hardly surprising that his tabulation of the *Aegocrioceras* fauna is a compilation of valid and invalid names, whose usage seems to vary from one collection to the next. Many of the extant collections which Spath examined bear little indication of his determinations, but the majority of the *Aegocrioceras* specimens in the Institute of Geological Sciences (formerly Geological Survey Museum) collections and a few of those in the British Museum (Natural History) have Spath identifications of proven pedigree. Thus his published records can be interpreted to a limited extent: Spath's 22 listed taxa are tabulated below, together with the catalogue numbers of specimens which he is known to have identified and their revised identification.

Spath's record	Cat. no.	Revised identification
<i>A. bucklandi</i> (Phillips) Buckland sp.	GSM. 32081	<i>A. sp. indet.</i>
<i>A. bucklandi</i> var. (Bean MS) (less compressed)	—	—
<i>A. capitanei</i> (Bean MS)	{ BM. C72670 GSM. 17495 GSM. 32096 }	<i>A. cf. varicosatum</i> <i>A. semicinctum</i> <i>A. cf. spathi</i>
<i>A. sp. nov. aff. capitanei</i> (Bean MS)	{ BM. C72704 GSM. 17479 GSM. 17498 }	<i>A. densiradiatum</i> (holotype) <i>A. densiradiatum</i> <i>A. densiradiatum</i> (paratype)
<i>A. capricornu</i> (Roemer)	BM. C72656-7	<i>A. bicarinatum</i>
<i>A. cristatum</i> Pavlow non d'Orb. sp.	—	—
<i>A. aff. cristatum</i> (Pavl. non d'Orb.)	{ GSM. 17478 GSM. 32080 }	<i>A. aff. bicarinatum</i> <i>A. bicarinatum</i>
<i>A. intermedium</i> (Phillips)	{ GSM. 17482, 17484-7, 17489, 17490, 17492, 17493, 32137 }	<i>A. varicosatum</i>
<i>A. intermedium</i> (Bean MS non Phillips)	BM. 89107	<i>A. bicarinatum</i> (neotype)
<i>A. sp. nov. ? aff. intermedium</i> ('cf. <i>duvali</i> ' Koenen in Danford)	GSM. 17475-6	<i>A. cf. bicarinatum</i>
<i>A. koeneni</i> sp. nov.	GSM. 32097	<i>A. sp.</i>
<i>A. ligatum</i> (Bean MS)	{ YM. 885, PR/1975/1 BM. 89101 }	<i>A. semicinctum</i> <i>A. sp. indet.</i>
<i>A. quadratum</i> (Bean MS) Crick sp.	BM. 89102, C7154	<i>A. quadratum</i> (syntypes)
<i>A. varicosatum</i> (Phillips)	—	—
<i>A. seeleyi</i> (Neumayr & Uhlig)	—	—
<i>A. semicinctum</i> (Roemer)	{ BM. C72653, GSM. 32090 GSM. 32074-5 GSM. 17477, 17537, 32124 }	<i>A. quadratum</i> <i>A. cf. quadratum</i> <i>A. bicarinatum</i>
<i>A. cf. semicinctum</i> (Roemer) (? = <i>insigne</i> Pictet)	—	—
<i>A. sp. nov. ? aff. semicinctum</i> (Roemer)	—	—
<i>A. subnodosum</i> (Roemer)	—	—
<i>A. subseeleyi</i> sp. nov.	{ GSM. 17540 YM. tablet 420 GSM. 17499, 32143 }	<i>A. bicarinatum</i> <i>A. cf. bicarinatum</i> <i>A. sp. juv.</i>
<i>A. torulosum</i> (Koenen)	BM. C72652	<i>A. quadratum</i>
<i>A. sp. nov.</i>	—	—

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P. F. RAWSON, B.Sc., Ph.D., F.G.S.
 Department of Geology
 QUEEN MARY COLLEGE (UNIVERSITY OF LONDON)
 MILE END ROAD
 LONDON E1 4NS

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